Aitchison, C. W. 1984. Low temperature feeding by winter-active spiders. J. Arachnol., 12:297-305.

LOW TEMPERATURE FEEDING BY WINTER-ACTIVE SPIDERS

C. W. Aitchison

Department of Entomology
University of Manitoba, Winnipeg
Manitoba R3T-2N2, Canada

ABSTRACT

Feeding by winter-active and winter-inactive species of spiders at low temperatures and the kinds of invertebrate prey eaten were determined. Winter-active spiders fed at 2°C, less often at -2°C and rarely at -5°C, whereas winter-inactive species displayed even more reduced feeding or none. All prey offered to the spiders were eaten except nabids, hymenopterans and the collembolan *Onychiurus pseudoarmatus.* In general, small spiders consumed small prey and larger spiders larger prey. Some scavenging was seen in large female spiders. The most probable prey of winter-active spiders are the winter-active collembolans, all of which inhabit the subnivean space and litter during winter.

INTRODUCTION

Feeding by ectothermic animals at temperatures near freezing may appear unlikely; however there is evidence that winter-active spiders feed upon winter-active collembolans on the snow surface (Polenec 1962, Buchar 1968, Hågvar 1973, Schaefer 1977). Many linyphiines, erigonines, lycosids, clubionids, thomisids, and tetragnathids are active during winter under litter and snow (Polenec 1962, Thaler and Steiner 1975, Schaefer 1976, 1977, Aitchison 1978, Flatz 1979, Puntscher 1979). An increased metabolic rate in these spiders may permit activity at low temperatures comparable to the two- to four-fold elevation of metabolism over the normal environmental temperature range seen in Antarctic mites (Block and Young 1978, Block 1980). Low threshold temperatures for activity by spiders do exist, below which activity ceases (Hågvar 1973, Aitchison 1978). Other researchers consider that accumulation of cryo-protectants permits activity (Hågvar 1973, Husby and Zachariassen 1980), but that feeding is incompatible with cold-hardiness since it introduces ice nucleators into the gut (Salt 1953). Nonetheless energy must be available to the winter-active organism in order to continue its mobility; possibly this energy is derived from stored lipids (Collatz and Mommsen 1974, Norberg 1978).

At temperatures below +5°C, and possibly with the metabolic rate somewhat depressed, there are fewer energy requirements and, as a consequence, less feeding. Below 5°C assimilated food is efficiently used (99%) by spiders, although many invertebrates, utilizing stored lipids, have a negative energy balance below that temperature (Moulder and Reichle 1972, Collatz and Mommsen 1974). Indeed, during the four months of the Swedish winter, the energy content of spiders was reduced by 13% (Norberg 1978). Feeding occurs at reduced levels at 2°C (Edgar 1971, Aitchison 1981) and as low as -4°C

Table 1.—List of winter-active and winter-inactive species of spiders from the vicinity of Winnipeg, Manitoba, Canada, collected in 1980 by means of litter extraction, sweeping of undergrowth and beating of bushes.

Family-group	Winter-active Species	Winter-inactive Species
Erigoninae	*Ceraticelus fissiceps* (Cbr.)	*Maso sundevalli* (Westring)
	Ceraticelus laetus Cbr.	undetermined juveniles
	Collinsia plumosa (Em.)	
	Diplocephalus cuneatus Em.	
	Gonatium crassipalpum Byrant	
	Grammonota pictillis (Cbr.)	
	undetermined juveniles	
Linyphiinae	*Centromerus sylvaticus* (Blw.)	
	Neriene clathrata Sundevall	
	undetermined juveniles	
Theridiidae		*Euryopsis argentea* Em.
		undetermined juveniles
Araneidae	*Araniella displicata* (Hentz)	*Nuctenea patagiata* (Cl.)
Tetragnathidae	*Pachygnatha* sp.	
Agelenidae		*Agelenopsis potteri* Blw.
Hahniidae	*Neoantistea magna* (Keys.)	
Pisauridae		*Dolomedes* sp.
Lycosidae	*Alopecosa aculeata* Cl.	*Pardosa fuscula* Thor.
	Pardosa distincta Blw.	
	Pardosa moesta Banks	
	Pirata sp.	
Gnaphosidae	*Haplodrassus hiemalis* (Keys.)	*Herpyllus ecclesiasticus* Hentz
	Zelotes sp.	
Clubionidae	*Agroeca ornata* Banks	
	Agroeca sp.	
	Castianeira sp.	
	Clubiona sp.	
Thomisidae	*Oxyptila sincera canadensis* Dondale & Redner	
	Oxyptila sp.	*Coriarachne utahensis* (Gertsch)
	Xysticus elegans Keys.	*Misumena vatia* (Cl.)
	Xysticus emertoni Keys.	undetermined juveniles
Philodromidae	*Thanatus* sp.	*Philodromus cespitum* (Walck.)
	Tibellus oblongus (Walck.)	
Salticidae		*Metaphidippus protervus* (Walck.)
		Pellenes hoyi (Peckham & Peckham)
		undetermined juveniles
Dictynidae	*Argenna obesa* Em.	*Dictyna minuta* Em.
		Dictyna sp.

(Gunnarsson 1983). Subadults of *Pardosa lugubris* (Walck.) subjected to 4°C for the winter period of inactivity took little food over the winter (Edgar 1971); whereas juveniles of *Coelotes atropos* (Walck.) fed readily at 6°C, less frequently at 4°C, and infrequently at 2°C. Generally, at low temperatures adults apparently eat more than do the juveniles (Aitchison 1981), possibly conferring an adaptive advantage to the overwintering juveniles which, by feeding less, have fewer nucleating agents for ice crystals in their guts.

There are other invertebrates which also feed at temperatures near freezing. Under stones in the Canadian Rocky Mountains, the orthopteroid *Grylloblatta campodeiformis*

Walker has full guts at temperatures between 0°C and 5°C, having consumed hardy collembolans and other arthropods (Pritchard and Scholefield 1978). Winter-active subnivean collembolans feed down to about -2.5°C (Aitchison 1983). At temperatures of about -1.5°C, a polar amphipod reproduces and grows, presumably feeding as well (Dunbar 1957), and at near 0°C the planktonic copepod *Centropages hamatus* (Lilljeborg) displays a low rate of food intake and an extremely efficient digestion (Kiørboe *et al.* 1982). Thus it appears that some feeding and efficient assimilation can occur during winter.

This study was undertaken to determine the differences in feeding by winter-active and winter-inactive spiders at temperatures near freezing, and the types of invertebrate prey eaten. The term WINTER-ACTIVE refers to horizontal mobility at low temperatures (2°C or lower) during winter months; and WINTER-INACTIVE refers to a lack of mobility, i.e., animals rarely, if ever, taken in pitfall traps during winter months.

MATERIALS AND METHODS

The spiders and prey were collected from the undisturbed grounds of the Canada Cement Lafarge Company, Fort Whyte, Manitoba, Canada (49°49′N, 97°13′W), and of the University of Manitoba (49°49′N, 97°8′W), by extraction from litter, beating of bushes and sweeping of undergrowth during the summer and autumn of 1980. The live spiders were identified and placed into the categories of winter-active and winter-inactive species (Table 1) (Aitchison 1984). The prey, with the exception of collembolans, were identified to family or order only. The collembolan species tested include *Isotoma viridis* Bourlet, *Proisotoma minuta* (Tullberg), *Lepidocyrtus violaceus* Fourcroy, *Orchesella ainslei* Folsom, *Tomocerus flavescens* Tullberg, *Entombrya* sp., *Hypogastrura* sp. and *Onychiurus pseudoarmatus* Folsom.

The 36 winter-active and 46 winter-inactive spiders, representing adults and juveniles of 40 species were kept at 8°C (± 1°C) for 60 days and then placed at 2°C (± 1°C). After 40 days, 20 winter-active and 7 winter-inactive spiders were placed at -2°C (± 1°C), and after 30 additional days 13 winter-active and 3 winter-inactive spiders were placed at -5°C (± 1°C). The animals held at -2°C stayed at that temperature for about five months, the length of time over which they would have encountered similar temperatures in the field; those spiders held at -5°C stayed at that temperature for a period of four months. The small number of experimental spiders was periodically augmented throughout the winter by animals collected from the field. Each spider was held in a 4-dram vial with 1 cm of damp sand in the bottom and fed weekly on one or two *Drosophila melanogaster* Mg. or collembolans, depending upon the size of the spider. Uneaten dead prey or remnants were removed at the time of feeding, and a few drops of water were added to the sand. Notations of prey remains and/or moults were made.

In the experiments to determine the prey eaten, spiders from the families Erigoninae, Lycosidae and Thomisidae were held at 10°C for two weeks without food and then provided with prey species collected from the field. No experiments were done at higher temperatures. Again the spiders were individually placed in vials, and the prey eaten were noted after 8, 24 and 48h. The same procedure was was used for the eight prey species of collembolans.

RESULTS

Low temperature feeding.—The small number of specimens (n = 82) involved did not permit comprehensive statistical analyses of these data, other than means and standard errors, both of which show considerable variability. At 2°C the winter-active specimens consumed a mean of 0.24 ± 0.15 prey/spider/10-day period (n = 36), compared to a mean of 0.03 ± 0.15 prey/spider/10 days (n = 46) for the winter-inactive spiders (Figure 1A). Some of the juvenile thomisids and salticids became torpid at this and lower temperatures. Females of *Agroeca* spp., *Grammonota pictilis* (Cbr.), unidentified linyphiines, and some juveniles of *Pardosa moesta* Banks and *Neoantistea* spp. were the most voracious feeders. After 110 days at 2°C, only active individuals fed, those being the following species, *Ceraticelus* spp., *Diplocephalus cuneatus* (Em.) and juveniles of *Pardosa distincta* (Blw.) and *Thanatus* spp. After 140 days at this temperature, some of the erigonines and linyphiines often had constructed skimpy webs, while other spiders had not made any.

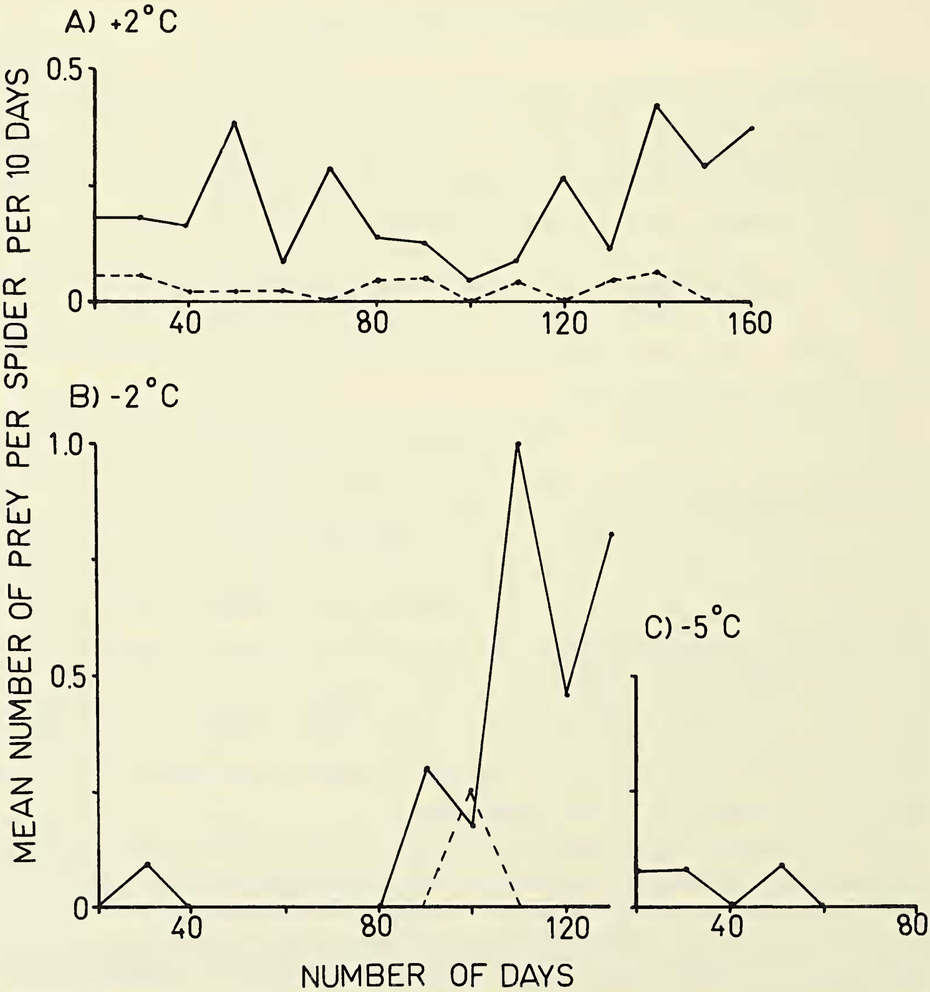

Fig. 1.—The mean number of prey eaten per spider per 10 day period at various temperatures: (A) at 2°C, (B) at -2°C, and (C) at -5°C. The winter-active spiders are represented by the solid line, and the winter-inactive spiders by the dotted line.

Table 2.–Prey eaten (+) and uneaten (-) by spiders of various families held at 10°C and starved two weeks; blanks represent untested combinations.

	Predator		
Prey	Erigoninae	Lycosidae	Thomisidae
Collembola	+	+	+
Aphidae	-	+	-
Cicadellidae		+	+
Nabidae		-	-
Other hemipterans		+	+
Orthoptera		+	
Lepidoptera		+	+
Hymenoptera		-	
Diptera	+	+	+
Coleoptera		+	-

The winter-active spiders showed approximately the same food consumption at -2°C and +2°C (0.24 ± 0.34 prey/spider/10 days (n = 20) and 0.24 ± 0.15 respectively) (Figure 1B), although feeding occurred less frequently until 6 May 1981 (day 110). After this date, consumption rose to a higher level, especially in the linyphiines and females of *Agroeca ornata* Banks, in spite of the temperature remaining constant. Several female *Centromerus sylvaticus* (Blw.), *Agelenopsis potteri* (Blw.) and *A. ornata* fed, laid eggs and then died. One erigonine produced a web after 60 days. By contrast to the winter-active species, the winter-inactive species consumed a mean of 0.02 ± 0.07 prey/spider/10 days (n = 7) at -2°C.

At -5°C the winter-active spiders consumed a mean of 0.03 ± 0.04 prey/spider/10 days (n = 13) whereas the winter-inactive individuals did not feed (Figure 1C). Only collembolans were used as prey since they remained active over the experimental feeding period for both groups. A juvenile *Pirata* produced a web platform after 35 days at -5°C and a partial web after 63 days.

Spiders collected in late September, i.e., juvenile salticids, one juvenile each of *Zelotes* sp., *Clubiona* sp., *Pirata* sp., and *P. moesta,* produced silken chambers 20 to 40 days after captivity, presumably in which to overwinter. These animals did not feed while in their overwintering chambers, in which they remained throughout the experiment.

Types of invertebrate prey.–All winter-active spiders consumed collembolans and dipterans. Lycosids also fed on aphids, cicadellids, other hemipterans, orthopterans, lepidopterans and coleopterans; and thomisids ate cicadellids, other hemipterans and lepidopterans (Table 2). Nabids were not accepted by any spider at 10°C. In addition, a female *Alopecosa aculeata* (Cl.) consumed a dead cicadellid and weevil, and a large juvenile *Xysticus* ate a dead fly.

The experiments with collembolan species as prey showed that *O. pseudoarmatus* was avoided (Table 3). All other collembolan species were eaten by various spiders, with the smaller erigonines and linyphiines probably restricted to smaller prey, except for an erigonine (2 mm long) feeding upon a 3 mm long *T. flavescens.* The smallest collembolan, *P. minuta* with a maximum length of 1 mm, was fed upon only by erigonines, linyphiines and small juveniles of other families.

Table 3.—Species of collembolans eaten (+) or rejected (-) by various families of spiders held at 10°C and starved two weeks; blanks represent untested combinations. *[Iv = Isotoma viridis, Op = Onychiurus pseudoarmatus, Hyp = Hypogastrura* sp., *Lv = Lepidocyrtus violaceus, Oa = Orchesella ainslei, Tf = Tomocerus flavescens, Ent = Entombrya* sp., and *Pm = Proisotoma minuta.]*

	Collembolan species							
Spider Family	*Iv*	*Op*	*Hyp*	*Lv*	*Oa*	*Tf*	*Ent*	*Pm*
Erigoninae	-	-	+	+	+	+	-	+
Linyphiinae	+		-	-	-	-	-	+
Lycosidae	+	-	+	-	+	+	+	
Hahniidae		-	-		+	+		
Clubionidae	+	-	+	+	+	+	+	+
Thomisidae	+	-	-	+	+	+	+	

DISCUSSION

Low temperature feeding.—Winter-active spiders were observed to feed infrequently at near zero temperatures, i.e., +2 and -2°C. In particular, the linyphiines, erigonines, and juvenile lycosids fed at those temperatures, as did some hahniids and clubionids. As corroboration, Gunnarsson (pers. comm.) noted that at about 4°C subadult linyphiines fed during winter and even increased their weight by 169%, but did not moult. Low temperature feeding by other arthropods also support these findings (Dunbar 1957, Pritchard and Scholefield 1978, Kiørboe *et al.* 1982, Aitchison 1983); thus cold-adapted animals may feed at temperatures near freezing, supporting the results here of occasional feeding by winter-active spiders at subzero temperatures.

Differences in responses of some juvenile *Xysticus* spp. and *Oxyptila* spp. to cold were noted, seemingly within one species at times. Under the same temperature conditions and with no feeding displayed at subzero temperatures, some individuals were moderately active, while others were torpid. Perhaps there are underlying variations between individuals with respect to survival: the more active ones would be better able to avoid predators, whereas the torpid ones would expend less energy. More research needs to be done into this area.

An interesting phenomenon occurred in feeding patterns, possibly caused by an unknown stimulus. Although kept at constant temperatures in dark incubators and offered prey once weekly, spiders showed increased feeding by mid- and late spring.

The overall metabolism of spiders at lower temperatures still permits some of them to spin silk and to moult. Overwintering in silken chambers is a mechanism used by pseudoscorpions (Gabbutt and Aitchison 1980), and especially by the salticids in this study, as well as some winter-active spiders—juvenile lycosids, clubionids and gnaphosids. In addition, one juvenile even moulted at 2°C.

It appears as though the winter-inactive spiders probably undergo a period of starvation during winter, some within silken chambers; whereas the winter-active spiders generally remain capable of locomotion, occasional feeding and infrequent moulting at near zero temperatures.

Types of invertebrate prey.—On the whole, spiders are opportunitistic feeders eating any abundant, palatable, and suitably-size prey in their immediate habitat. In the litter at

the soil surface the most abundant small invertebrates are the thin-cuticled collembolans, especially of the genera *Orchesella* and *Tomocerus,* which comprise up to 50% of the prey of lycosids, erigonines and linyphiines (Moulder and Reichle 1972, Nyffeler and Benz 1979a, 1981). Small spiders in rigorous environments feed on saprovores and detritivores, including small mites, collembolans, and dipterans, and altogether represent stunted food chains (Otto and Svensson 1982). Certainly the subnivean environment is rigorous with its subzero temperatures, and the food chains are consequently stunted, presenting mostly winter-active collembolans to the spiders as prey (Aitchison 1979).

Some potential prey are unpalatable for arachnids, such as some podurid and onychiurid collembolans which secrete repellents (Huhta 1971). *Onychiurus pseudoarmatus* were left untouched in these experiments, as were collembolans of the same genus offered to the pseudoscorpion *Apochthonius minimus* (Schuster) (Johnson and Wellington 1980).

In this study, collembolans greater than 1 mm were eaten whereas the small *P. minuta* may have been ignored as insignificant prey by the larger spiders which did not eat this species. Both the small erigonines and linyphiines, representative of the size of most winter-active species, consumed *P. minuta* as prey. A size range of 0.25 to 0.75 times the body length of the predator (Nentwig 1982) or 0.05 to 0.17 the predator's size (Huhta 1971) is considered an "ideal" prey size. Most of the prey of linyphiines and erigonines have a mean length of 1.5 mm and a maximum of 3 mm (Nentwig 1980), and the size range of some lycosid prey is 1 to 3 mm (Nyffeler 1982)--all within the average size range of collembolans.

Among the most commonly attacked prey of epigean spiders are dipterans, aphids, collembolans, other insects and smaller spiders. In the chelicerae of field-captured, cursorial *Pardosa* spp. were up to 28.6% collembolans and 33.3% aphids, whereas epigean *Xysticus* spp. caught only 5.7% collembolans and 11.4% aphids (Nyffeler and Benz 1979b). Over 85% of the prey in the chelicerae of hand-captured *P. lugubris* were in the collembolan genera *Orchesella* and *Tomocerus,* or were small dipterans (Nyffeler and Benz 1981). With the exception of the erigonines, the experimental spiders did feed on dipterans, aphids and collembolans.

The litter fauna of this study area consisted predominantly of small species of spiders and collembolans, with the latter probably prey of the former. Certainly these insects were generally well accepted as prey by the spiders. This agrees with the results of Nyffeler (1982) and Wingerden (1977), in which linyphiines and erigonines fed upon collembolans of the genera *Orchesella, Lepidocyrtus* and *Isotomurus,* all of which the spiders here also accepted as prey.

Among the winter-active subnivean fauna in southern Canada, the collembolans and spiders represent much of the invertebrate fauna (Aitchison 1978, 1979). This study ascertained that spiders do feed down to -2°C and that collembolans are accepted as prey, so when temperatures under snow are at that temperature or higher, spider predation upon collembolans may occur. Elsewhere winter-active spiders have been seen consuming collembolans and small dipterans (Polenec 1962, Buchar 1968, Hågvar 1973, Schaefer 1976), further supportive of this study. This potential prey of winter-active spiders most probably consist mainly of Collembola.

ACKNOWLEDGMENTS

I wish to thank Canada Cement Lafarge Company for the use of its undisturbed grounds; Canada Agriculture Research Station for laboratory space; L. B. Smith for his

supervision; W. Nentwig, S. Toft, O. Morris, S. R. Loschiavo and K. Thaler for comments on the manuscript: C. D. Dondale and J. Redner for determinations of spider species; A. Fjellberg, K. Christiansen and R. M. Snider for determinations of collembolans; F. Kozin and M. Novak for translations of Slovenian and Czech respectively; and A. Shukla for typing. The research was partially funded by a University of Manitoba Research Grant (no. 431-1119-60).

LITERATURE CITED

Aitchison, C. W. 1978. Spiders active under snow in southern Canada. Symp. Zool. Soc. Lond., 42:139-148.

Aitchison, C. W. 1979. Winter-active subnivean invertebrates in southern Canada. I. Collembola. Pedobiologia, 19:113-120.

Aitchison, C. W. 1981. Feeding and growth of *Coelotes atropos* (Agelenidae, Araneae) at various temperatures. J. Arachnol., 9:327-330.

Aitchison, C. W. 1983. Low temperature and preferred feeding by winter-active collembolans. Pedobiologia, 25:27-36.

Aitchison, C. W. 1984. The phenology of winter-active spiders. J. Arachnol., 12:

Block, W. 1980. Survival strategies in polar terrestrial arthropods. Biol. J. Linn. Soc., 14:29-38.

Block, W. and S. R. Young. 1978. Metabolic adaptations of Antarctic terrestrial micro-arthropods. Comp. Biochem. Physiol., 61A:363-368.

Buchar, J. 1968. [A winter trip among spiders.] In Czech. Ziva, 16: 24-25.

Collatz, K.-G. and T. Mommsen. 1974. Lebenweise und jahreszyklische Veränderungen des Stoffbestandes der Spinnen *Tegeneria atrica* C. L. Koch (Agelenidae). J. Comp. Physiol., 91:91-109.

Dunbar, M. J. 1957. The determinants of production in northern seas: a study of the biology of *Themisto libellula* Mandt., "Calanus" Series no. 14. Canadian J. Zool., 35:797-819.

Edgar, W. D. 1971. Aspects of the ecological energetics of the wolf spider *Pardosa (Lycosa) lugubris* (Walckenaer). Oecologia, 7:136-154.

Flatz, S. 1979. Winteraktivität epigäischer Arthropoden (ibs. Aranei, Carabidae) im Bereich der Landesanstalt für Pflanzenzucht und Samenprüfung Rinn (Nordtirol, 900 mNN). Mag. Thesis, Universität Innsbruck, Austria. 75 pp.

Gabbutt, P. D. and C. W. Aitchison. 1980. The effect of temperature and season on the number of hibernation chambers built by adult pseudoscorpions. Proc. 8th Internat. Arachnologen-Kongress, Wien, pp. 57-60.

Gunnarsson, B. 1983. Winter mortality of spruce-living spiders: effect of spider interaction and bird predation. Oikos, 40:226-233.

Hågvar, S. 1973. Ecological studies on a winter-active spider *Bolyphantes index* (Thorell) (Araneida, Linyphiidae). Norsk entomol. Tiddskr., 20:309-314.

Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Ann. Zool. Fennici, 8:483-542.

Husby, J. A. and K. E. Zachariassen. 1980. Antifreeze agents in the body fluid of winter-active insects and spiders. Experientia, 36:963-964.

Johnson, D. L. and W. G. Wellington. 1980. Predation of *Apochthonius minimus* (Pseudoscorpionida: Chthonidae) on *Folsomia candida* (Collembola: Isotomidae). I. Predation rate and size-selection. Res. Pop. Ecol. 22:339-352.

Kiørboe, T., F. Møhlenberg and H. Nicolajsen. 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food consumption and temperature. Ophelia, 21:181-194.

Moulder, B. C. and D. E. Reichle. 1972. Significance of spider predation in the energy-dynamics of forest-floor arthropod communities. Ecol. Monog., 42:473-498.

Nentwig, W. 1980. The selective prey of linyphiid-like spiders and their space webs. Oecologia (Berl.), 45:236-243.

Nentwig, W. 1982. Epigeic spiders, their potential prey and competitors: relationship between size and frequency. Oecologia (Berl.), 55:130-136.

Norberg, R. Å. 1978. Energy content of some spiders and insects on branches of spruce *(Picea abies)* in winter; prey of certain passerine birds. Oikos, 31:222-230.

Nyffeler, M. 1982. Field Studies on the Ecological Role of the Spiders as Insect Predators in Agroecosystems (abandoned grassland, meadows, and cereal fields). Doctoral thesis, Swiss Federal Institute of Technology, Zurich. 174 pp.

Nyffeler, M and G. Benz. 1979a. Jahreszeitliches und räumliches Verteilungsmuster sowie Nahrungsökologie der dominanten epigäischen Spinnen von Winterweizenfeldern (Bodenfallenanalysen und Freilandbeobachtungen). Mitt. der Schweiz. Entomol. Gesell., 52:444-445.

Nyffeler, M. and G. Benz. 1979b. Nischenüberlappung bezüglich der Raum- und Nahrungskomponenten bei Krabbenspinnen (Araneae: Thomisidae) und Wolfspinnen (Araneae: Lycosidae) in Mähweisen. Rev. suisse Zool., 86:855-865.

Nyffeler, M. and G. Benz. 1981. Freilanduntersuchungen zur Nahrungsökologie der Spinnen: Beobachtungen aus des Region Zürich. Anz. Schädlingskde., Pflanzenschutz, Umweltschutz, 54:33-39.

Otto, C. and B. S. Svensson. 1982. Structure of communities of ground-living spiders along altitudinal gradients. Holarctic Ecol., 5:35-47.

Polenec, A. 1962. [Winterspinnen aus Mala Hrastnica.] In Slovenian. Loški Razgledi, 9:66-70.

Pritchard, G. and P. Scholefield. 1978. Observations on the food, feeding behavior, and associated sense organs of *Grylloblatta campodeiformis* (Grylloblattodea). Canadian Entomol., 110:205-212.

Puntscher, S. 1979. Verteilung und Jahresrhythmik von Spinnen im Zentralalpinen Hochgebirge (Obergurgl, Ötztaler Alpen). Doctoral dissertation, Universität Innsbruck, Austria. 117 pp.

Salt, R. W. 1953. The influence of food on cold-hardiness of insects. Canadian Entomol., 85:261-269.

Schaefer, M. 1976. Experimentelle Untersuchungen zum Jahreszyklus und zur Überwinterung von Spinnen (Araneida). Zool. Jb. Syst., 103:127-289.

Schaefer, M. 1977. Winter ecology of spiders (Araneida). Z. angew. Entomol., 2:113-134.

Thaler, K. and H. M. Steiner. 1975. Winteraktive Spinnen auf einem Acker bei Grossenzerdorf (Niederösterreich). Anz. Schädlingskde., Pflanzenschutz, Umweltschutz, 48:184-187.

Wingerden, W. K. R. E. van. 1977. Population Dynamics of *Erigone arctica* (White) (Araneae, Linyphiidae). Doctoral thesis, Free University of Amsterdam. 147 pp.

Manuscript received July 1983, revised January 1984.